

ORIGINAL PAPER

A. C. Franco · A. G. de Soyza · R. A. Virginia
J. F. Reynolds · W. G. Whitford

Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*

Received: 12 March 1993 / Accepted: 15 November 1993

Abstract *Larrea tridentata* is a xerophytic evergreen shrub, dominant in the arid regions of the southwestern United States. We examined relationships between gas-exchange characteristics, plant and soil water relations, and growth responses of large versus small shrubs of *L. tridentata* over the course of a summer growing season in the Chihuahuan Desert of southern New Mexico, USA. The soil wetting front did not reach 0.6 m, and soils at depths of 0.6 and 0.9 m remained dry throughout the summer, suggesting that *L. tridentata* extracts water largely from soil near the surface. Surface soil layers (<0.3 m) were drier under large plants, but pre-dawn xylem water potentials were similar for both plant sizes suggesting some access to deeper soil moisture reserves by large plants. Stem elongation rates were about 40% less in large, reproductively active shrubs than in small, reproductively inactive shrubs. Maximal net photosynthetic rates (P_{\max}) occurred in early summer ($21.3 \mu\text{mol m}^{-2} \text{s}^{-1}$), when pre-dawn xylem water potential (XWP) reached ca. -1 MPa . Although both shrub sizes exhibited similar responses to environmental factors, small shrubs recovered faster from short-term drought, when pre-dawn XWP reached about -4.5 MPa and P_{\max} decreased to only ca. 20% of unstressed levels. Gas

exchange measurements yielded a strong relationship between stomatal conductance and photosynthesis, and the relationship between leaf-to-air vapor pressure deficit and stomatal conductance was found to be influenced by pre-dawn XWP. Our results indicate that stomatal responses to water stress and vapor pressure deficit are important in determining rates of carbon gain and water loss in *L. tridentata*.

Key words Gas-exchange · *Larrea tridentata*
Phenology · Stomatal conductance · Water relations

Introduction

Creosotebush (*Larrea tridentata* [D.C.]Cov.), an evergreen perennial shrub, is dominant throughout the Mojave, Sonoran and Chihuahuan Deserts of the southwestern United States (Shreve 1942). The success of creosotebush in these arid environments may be attributed in part, to its ability to photosynthesize throughout the year (Oechel et al. 1972a, b; Reynolds 1986), giving it an advantage over deciduous plants that have a shorter growing period and a lag period between the onset of conditions favorable to growth and the addition of new biomass. This maintenance of physiological function during drought is related to the ability of creosotebush to photosynthesize at very low xylem water potentials (XWP), even at pre-dawn XWP as low as -8 MPa (Odening et al. 1974). Creosotebush has also been shown to exhibit almost complete turgor maintenance over a wide range of water potentials (Meinzer et al. 1986). These characteristics may serve to diminish or delay the effects of water stress in this species.

Stomatal conductance can be a major rate-determining component of photosynthetic gas-exchange. Although creosotebush shrubs with low XWP have reduced rates of photosynthesis, it has not been determined whether or not these reductions in photosynthesis are a direct result of stomatal closure. Mooney et al. (1978) observed a seasonal shift in the temperature dependence of light saturated photosynthesis in creosote-

A. C. Franco
Departamento de Botanica, caixa postal 04631,
Universidade de Brasilia,
Brasilia, DF 70910, Brazil

A. G. de Soyza
Department of Biology, New Mexico State University,
Las Cruces, NM 88003, USA

R. A. Virginia (✉)
Environmental Studies Program, Dartmouth College,
Hanover, NH 03755, USA

J. F. Reynolds
Department of Botany, Duke University,
Durham, NC 27708, USA

W. G. Whitford
USEPA Environmental Monitoring Systems Laboratory,
P O Box 93478,
Las Vegas, NV 89193, USA

bush, but stomatal conductance (g_s) was little affected by temperature. Other studies have investigated seasonal photosynthetic patterns (Strain 1969, 1970; Oechel et al. 1972a), the effects of drought on turgor and osmotic relations (Monson and Smith 1982; Meinzer et al. 1986; Meinzer et al. 1988) and the relationships of net photosynthesis and water-use efficiency to leaf nitrogen content (Lajtha and Whitford 1989).

Although water is the major factor limiting establishment and growth of creosotebush (Sheps 1973; Cunningham et al. 1979; Sharifi et al. 1988), there is no information on what implications plant size might have on gas exchange and water use of this species. In general, smaller plants in the juvenile life-history stage have lower xylem water potentials and less efficient use of water. For some woody perennials these lower xylem water potentials of juveniles were accompanied by lower gas exchange rates (Brown and Archer 1990; Cui and Smith 1991), but not for *Chrysothamnus nauseosus*, a winter deciduous shrub of the Great Basin Desert (Donovan and Ehleringer 1992). These differences in water use may be related to differences in rooting depth between small and large shrubs. Large shrubs may be able to redirect a large portion of the intercepted rainfall via stem flow along root channels (Pressland 1976; Nulsen et al. 1986) and may be effectively decoupled from short-term fluctuations in water availability.

The objectives of this study were (1) to examine the degree of coupling of photosynthetic gas-exchange characteristics, water relations, and growth responses of small vs. large shrubs over the course of a summer growing season in the Chihuahuan Desert; (2) to examine the implications of stomatal responses to water stress and vapor pressure deficit on the rates of net CO_2 exchange of creosotebush.

Methods

Study site

This study was performed between July and October 1991 on the New Mexico State University College Ranch in the Jornada basin of the Chihuahuan Desert, 40 km NNE of Las Cruces, New Mexico, USA. The study site is in an extensive stand of creosotebush (*Larrea tridentata*) on a northeast-facing piedmont slope of Mt. Summerford, the northernmost peak of the Dona Ana Mountain range. These coarse-loamy soils have a calcic horizon within the upper two meters and a pH of 7 to 7.5 in 1 N KCl (Nash and Daugherty 1990). The climate is semiarid with a mean annual rainfall of 218 mm, about 60% occurring as late summer rainfall from brief convective storms (Kunkel et al. 1990). Summer maximum air temperatures reach 40° C, while freezing temperatures have been recorded from October to mid-April (Data from the Jornada LTER weather station).

Size class criteria

Larrea tridentata can grow as either a single stemmed shrub or in multistemmed clumps. We considered each clump (defined as any number of stems forming a discrete canopy) to represent a single shrub. Root excavations have shown that neighboring clumps are not connected, although their root systems may overlap to some

extent (Cannon 1911; Ludwig 1977). Thirty-two small shrubs and 32 large shrubs were selected from the population. We used plant height and litter accumulation under the shrubs as the main criteria to select and assign plants to the two size classes. From these, eight small and eight large plants were selected at random. To minimize the effect of neighboring shrubs on the water relations of the selected plants, approximately 0.6 m from the edge of the canopy, four 1-m deep trenches were cut to form a square around the selected plant. The trench was lined with black plastic, and the soil was returned. In an attempt to reduce the impact of root damage on the water relations of the plants, these trenches were done several months before measurements were first taken. The plants apparently recovered from any root damage, as indicated by the high pre-dawn water potentials and stomatal conductances measured in July (Figs. 1 and 3), typical of unstressed plants. Canopy volume (calculated as a cone) and height of small plants averaged $0.02 \pm 0.006 \text{ m}^3$ and $0.36 \pm 0.058 \text{ m}$ respectively, and $1.51 \pm 0.256 \text{ m}^3$ and $1.32 \pm 0.073 \text{ m}$ for large plants.

Gas-exchange and water relations

Diurnal photosynthetic gas-exchange was measured on eight days during the study (24 and 31 July; 12 and 26 August; 3, 9 and 26 September; 9 October), using a LI 6200 Portable Photosynthesis System (LI-COR Inc., Lincoln, NE). These days were selected to represent early, mid- and late summer conditions of the growing season. During each daily cycle, two terminal, sunlit branches of three or four plants out of the eight plants belonging to each size class were selected. Errors in ambient vapor pressure deficit (VPD), caused by heating of the cuvette, were corrected for by estimating VPD from measurements of relative humidity (RH) and air temperature (T_{air}) under shade, taken before and after each measurement cycle. Because desert perennials with small leaves such as *L. tridentata* have leaf temperatures close to air temperature (Smith 1978), leaf-to-air VPD was obtained by subtracting ambient vapor pressure from saturation vapor pressure at T_{air} .

As an indicator of plant internal water status, pre-dawn XWP was determined with a model 3005-1442 Plant Water Status Console (Soil Moisture Corp., Santa Barbara, CA) on one (small plants) or two (large plants) terminal branches of the same plants used for the gas exchange measurements. The size of the small plants limited the number of samples (replicates) we could take.

To determine soil water availability, pre-dawn soil water potential (SWP) at a depth of 0.2 m was determined with soil psychrometers (model PST-55-30-SF, Wescor Inc., Logan, UT), installed on the south side of the plant, near the edge of the canopy of 5 of the 8 plants of each size class. Before installation, each sensor was calibrated in 0.05, 0.5, 1.0 and 1.5 molal NaCl solutions, and a linear regression relating voltage to water potential was calculated for each sensor. Field measurements were corrected for temperature at the time of sampling.

Volumetric soil water content (SWC) was determined by the neutron attenuation technique using a CPN 503DR hydroprobe (CPN Corp., Santa Barbara, CA). Aluminium access tubes for the hydroprobe were installed near the edge of the canopy of each plant on the south side, and measurements were taken at 0.3, 0.6 and 0.9 m depth. Soil water content and pre-dawn XWP and SWP were determined on the same day that gas exchange was measured.

Two-way analysis of variance was used to examine the effects of plant size and sampling time on pre-dawn SWP, SWC and pre-dawn XWP.

Plant growth

To investigate plant growth, three stems were selected at random on each of the 16 plants, tagged with yarn, and marked at 0.05 m from the apex with enamel paint during July 1991, when initial measurements were taken. The length of all marked stems, the number of new nodes and the number of leaves for the new nodes

were recorded in August and in October 1991. The plants were monitored every two weeks for the presence of reproductive structures.

Results

Water relations

Total precipitation for the period of July 1 through October 30 1991 was 239.4 mm, 69% occurring during July and August (Fig. 1A). Long-term averages are not available for this site, but this value is more than the 97-year average annual rainfall of 217.9 mm recorded in the city of Las Cruces and almost double the average of 132.1 mm for the July to October period (Kunkel et al. 1990). September and October were much cooler than July and August, and minimum air temperature was below zero on October 31 (not shown).

Pre-dawn SWP at a depth of 0.2 m and pre-dawn XWP showed similar patterns over the growth season,

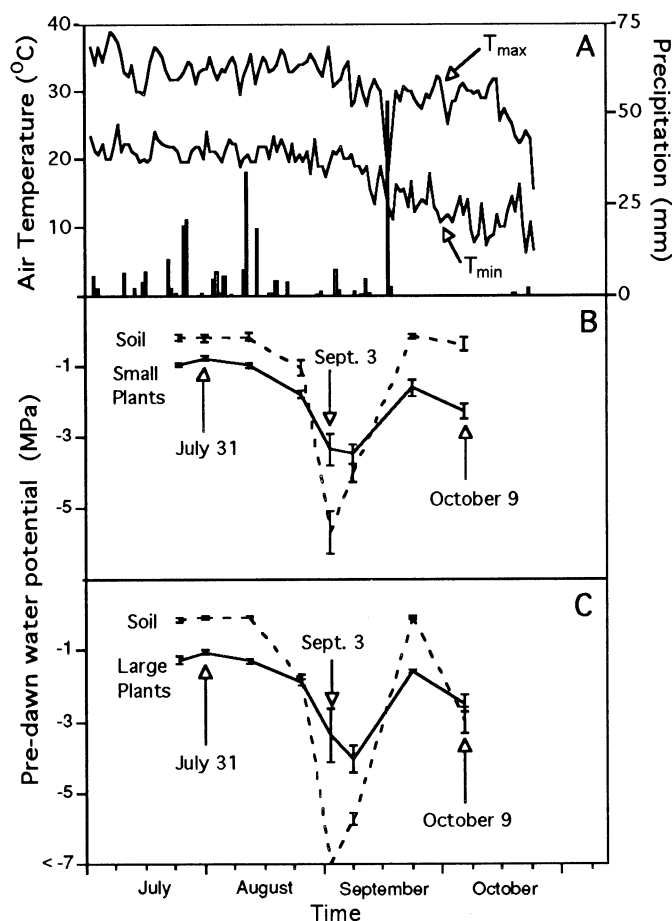


Fig. 1 A Changes in maximum and minimum air temperatures and rainfall events. B Changes in pre-dawn soil water potentials ($n = 5 \pm \text{SE}$) at 0.2 m depth and pre-dawn xylem water potentials ($n = 3$ or 4 plants $\pm \text{SE}$) for small, establishing shrubs. C Changes in pre-dawn soil water potentials at 0.2 m depth and pre-dawn xylem water potentials for large, established shrubs. The arrows indicate the days that are described in Fig. 3

and closely followed the pattern of rainfall (Figs. 1B and 1C). During the drier period from late August to the middle of September, SWP rapidly decreased to a minimum of less than -7 MPa under large plants and -5.7 MPa under small plants, while pre-dawn XWP reached -4.0 MPa for large plants and -3.5 MPa for small plants (Figs. 1B, C). Both SWP and XWP increased markedly following a 52.3 mm rainfall event on September 18, 1991. Soils under large plants had significantly lower ($P < 0.0001$) pre-dawn SWP, whereas pre-dawn XWP was not significantly different between size classes ($P = 0.17$). During wet periods, pre-dawn XWP was lower than SWP, but during dry periods SWP at 0.2 m was lower than XWP.

The intense summer convective storms typical of this region produced rapid runoff and low soil infiltration. Most soil wetting occurred at depths above 0.3 m (Figs. 1A, B and 2A, B). At this depth, volumetric SWC was significantly higher ($P < 0.0001$) under small plants, where it reached a maximum of 6.5%, compared to 4.9% under large plants (Fig. 2A, B). Soil at depths of 0.6 and 0.9 m remained dry (SWC $< 2.0\%$) during the summer.

As expected there was a significant time effect ($P < 0.0001$) on SWC, XWP and SWP. The plant size \times time interaction was significant for SWP ($P < 0.0001$), but not for SWC ($P = 0.13$) and XWP ($P = 0.98$).

Gas exchange

Diurnal patterns of T_{air} , leaf-to-air VPD, photosynthetic photon flux density (PPFD) and gas exchange for small

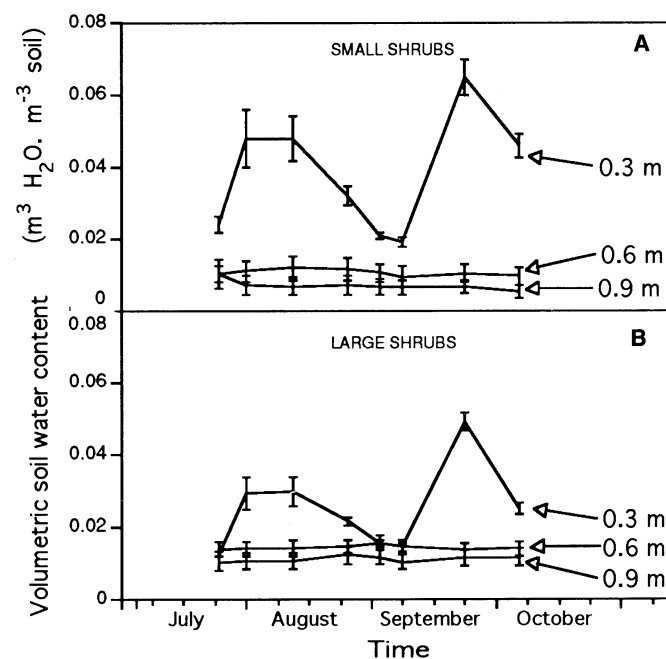


Fig. 2A, B Changes in volumetric soil water content ($n = 8 \pm \text{SE}$) at three different depths for small (A) and large (B) shrubs. Readings were taken near the edge of the canopy of each plant

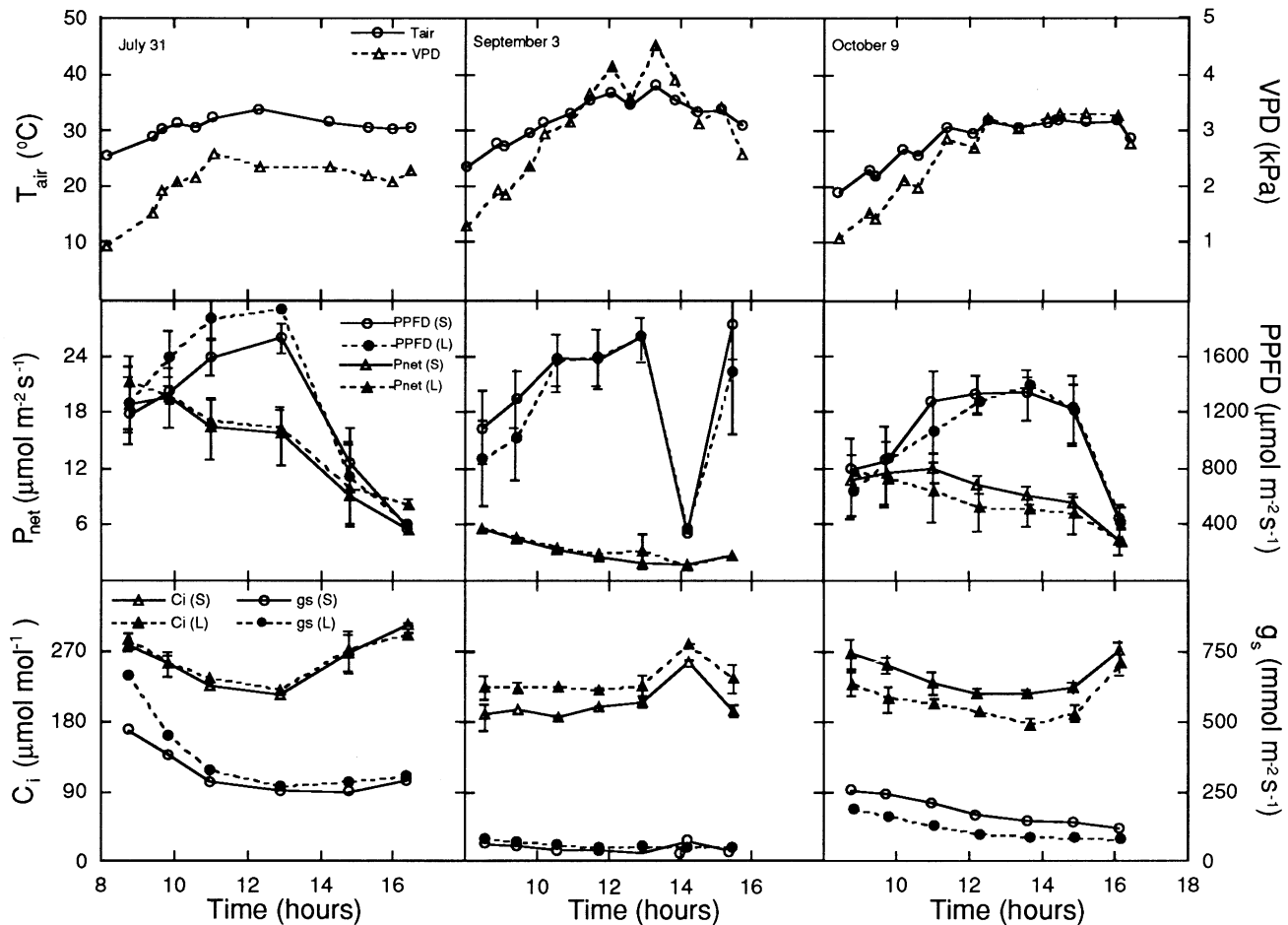
and large plants on three days, representative of our season-long data, are shown in Figure 3. On July 31, during the wet period, pre-dawn XWP averaged -0.82 MPa for small plants and -1.06 MPa for large plants (Fig. 1B, C). Gas exchange patterns and rates were similar for both plant sizes. Maximum values of net photosynthesis (P_{\max}) stomatal conductances and intercellular CO_2 concentrations occurred early in the day, when net photosynthesis rates reached 18.8 and $21.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, for small and large plants respectively. This 15% higher P_{\max} of large plants was accompanied by a 42% higher g_s . The steady increase in T_{air} , leaf-to-air VPD and PPFD levels throughout the morning was accompanied by a marked decrease in stomatal conductances. The decrease in intercellular CO_2 concentrations (C_i) and net photosynthetic rates was not as substantial. Stomatal conductance, T_{air} and leaf-to-air VPD remained fairly constant during the afternoon hours, while C_i increased. Thus, most of the afternoon decrease in photosynthetic rate was apparently the result of the marked decrease in PPFD levels.

On September 3, during the drought period, pre-dawn XWP reached ca. -3.3 MPa in both size classes. On this day, T_{air} and leaf-to-air VPD reached their highest recorded values. For both small and large plants, P_{\max} decreased to about $5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$, only ca. 28% of the July rates. Stomatal conductances

showed a decrease of similar magnitude, whereas C_i remained at about 180 and $200 \mu\text{mol mol}^{-1}$ for small and large plants respectively, during most of the day. By the end of the summer growing season (October 9), photosynthetic rates and stomatal conductances recovered somewhat, especially for small plants. Although pre-dawn XWP were similar for both size classes (Fig. 1B, C), small plants had higher net photosynthetic rates, stomatal conductances and intercellular CO_2 concentrations throughout most of the day (Fig. 3).

The P_{\max} of both large and small plants was related to pre-dawn XWP (Fig. 4). Values of P_{\max} decreased steadily from a high of nearly 28 to a low of $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ as XWP decreased from ca. -1 to -3 MPa. Further decreases in XWP did not result in a lower P_{\max} (Fig. 4). Stomatal conductances were linearly related to leaf-to-air vapour pressure deficit (Fig. 5). This relationship was apparently influenced by pre-dawn XWP. At any specific leaf-to-air VPD, g_s declined with decreasing pre-

Fig. 3 Diurnal courses of air temperature (T_{air}), leaf-to-air vapor pressure difference (VPD), photosynthetic photon flux density (PPFD), net photosynthesis (P_{net}), stomatal conductance (g_s), and leaf-internal CO_2 concentration (C_i) for small and large shrubs on three days, July 31 (sunrise 6:24 AM), September 3 (sunrise 6:46 AM), and October 9 (sunrise 7:08 AM), as described in the text. Standard errors of the means ($n=3$ or 4 plants) are shown for PPFD, P_{net} , g_s , and C_i .



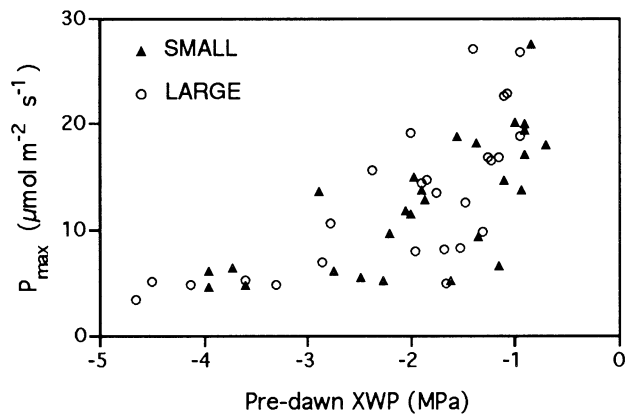


Fig. 4 Relationship between decreasing pre-dawn xylem water potential and maximum net photosynthesis (P_{\max}) for small (\blacktriangle) and large (\circ) shrubs

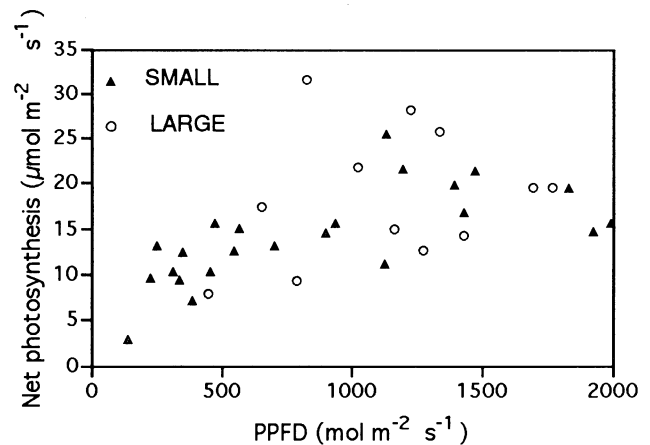


Fig. 6 Relationship between photosynthetic photon flux density (PPFD) and net photosynthesis for small and large shrubs. Data collected early morning (leaf-to-air vapor pressure deficit was less or equal to 0.9 kPa), for days that had pre-dawn xylem water potentials of less than -1.1 MPa

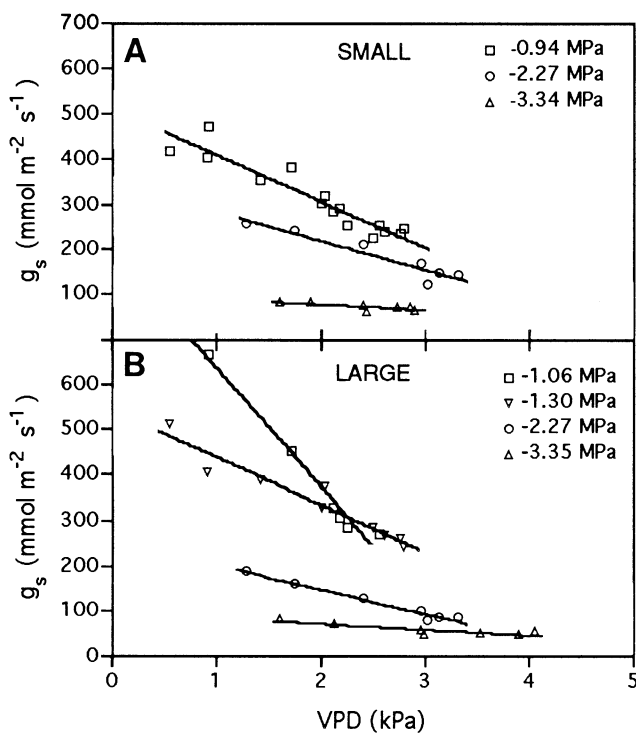


Fig. 5A, B Linear least-squares regressions on the relationship between stomatal conductance and leaf-to-air vapor pressure difference for small (**A**) and large (**B**) shrubs having different pre-dawn xylem water potentials. Each regression is based on measurements from a different day, and each point is the mean of six to eight branches from three to four plants (two branches per plant). Regressions were significant ($P < 0.001$) for small plants ($\square r^2 = 0.87$; $\circ r^2 = 0.86$; $\triangle r^2 = 0.89$) and for large plants ($\square r^2 = 0.97$; $\nabla r^2 = 0.92$; $\circ r^2 = 0.98$; $\triangle r^2 = 0.81$)

dawn XWP. Because the slope of the VPD response curve also declined with decreasing pre-dawn XWP, the effect was greater at low leaf-to-air VPD (high g_s).

We investigated the relationship between photosynthesis and PPFD by considering data from days when

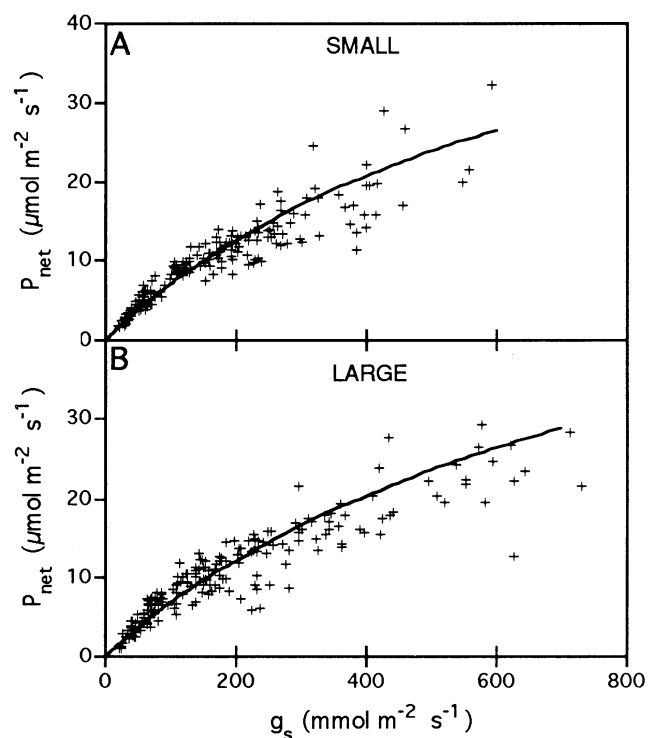


Fig. 7A, B Relationship between stomatal conductance (g_s) and net photosynthesis (P_{net}) at PPFD values above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data are for small (**A**) and large (**B**) shrubs. Data from all eight measurement days are shown, and each point is a single measurement. Linear regressions of the inverse of P_{net} and g_s yielded $P_{\text{net}}^{-1} = 1.6136 \times 10^{-2} + 12.736 \times g_s^{-1}$, $r^2 = 0.93$ for small shrubs and $P_{\text{net}}^{-1} = 1.5669 \times 10^{-2} + 13.345 \times g_s^{-1}$, $r^2 = 0.83$ for large shrubs. Both regression equations were significant ($P < 0.001$)

plants were not water stressed (i.e., pre-dawn XWP > -1.1 MPa), and VPD was fairly high, (0.6 to 0.9 kPa). Net photosynthetic rates apparently became light saturated at 1000 to 1250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD in large and small plants (Fig. 6). At PPFD values above 1000 μ

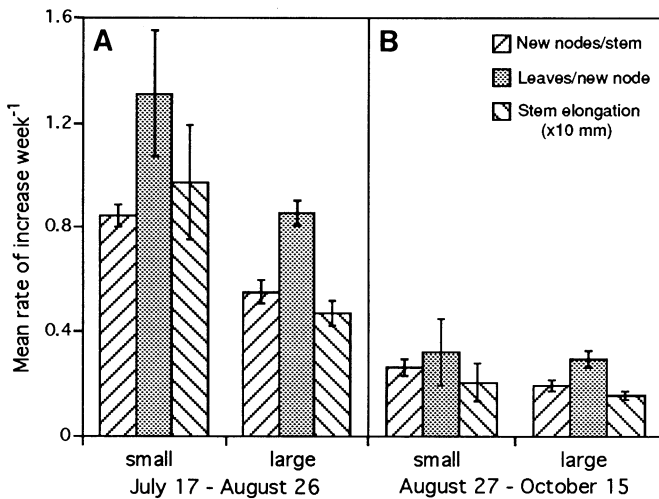


Fig. 8A, B Mean new node production per stem, leaf production for the new nodes and stem elongation for three branches on small and large shrubs during mid-season (A) and at the end of the growing season (B)

$\text{mol m}^{-2} \text{s}^{-1}$, there was a strong relationship between stomatal conductance and net photosynthesis (Fig. 7). The regression equations were similar for both plant sizes.

Growth and phenology

Mean stem elongation during the period of study was 6.7 mm for small plants and 4.0 mm for the large shrubs. Most stem elongation, leaf production and increase in number of nodes occurred during the months of July and August (Fig. 8). Large plants produced fewer nodes, fewer leaves per node and showed less branch elongation than did small plants (Fig. 8). These differences between plant size classes were statistically significant (*t* test, $P < 0.05$). During the months of September and October, both plant size classes showed a considerable reduction in branch elongation rates, in new node production and in the number of new leaves per node. Decrease in growth rate was greatest in the small plants, resulting in a reduction of the difference between small and large plant growth rates. The large shrubs all bore fruit throughout the period of measurement, but bore flowers only during July and August. Only half of the small shrubs produced reproductive structures, and not more than four reproductive structures were present on a small plant at any given time.

Discussion

Despite the unusually high precipitation during the study, the soil wetting front was restricted to depths above 0.6 m, perhaps due to substantial run-off following intense summer thunderstorms coupled with high evaporation rates. There was relatively little available water throughout the summer at depths of 0.6 and 0.9

m, because the measured SWC's of less than 2.0% using moisture release curves translate to SWP values below -7 MPa (Paul R. Kemp, personal communication). Schlesinger et al. (1987) in a nearby site have shown that although some soil moisture recharge occurred at depths of 0.35 and 0.70 m following fall and winter rains, this water was rapidly depleted early in the growing season, and soil at these depths remained dry throughout the summer. We can therefore assume that most of the water used by creosotebush in the summer is from the upper 0.6 m of the soil profile. This agrees with measurements of root distribution that showed most roots of creosotebush were within the first half meter of the soil, although some roots can extend to depths of at least 3 m (Freckman and Virginia 1989). Some measurements of SWC's at depths of 1.3 m in nearby creosotebush areas have indicated that SWC's at these depths remained fairly constant during the summer at about 6.6% (Virginia and Jarrel, unpublished data). It appears that creosotebush has access to deep soil water, which we could not detect. While water from these deep sources is unlikely to be available in quantities large enough to completely relieve water stress, it may be sufficient to allow the plant to remain active and maintain a positive carbon-balance during summer droughts. By maintaining some physiological activity during these periods of drought, creosotebush can more rapidly respond to precipitation events. Indeed, by the end of summer, soil re-wetting was accompanied by increased g_s and pre-dawn XWP.

The maximum pre-dawn XWP of -1 MPa found here is much higher than the -2 to -3 MPa reported for irrigated and nonirrigated plants in the Sonoran Desert of California (Oechel et al. 1972; Meinzer et al. 1988), or for this same site in other years (Syvertsen et al. 1975; Fonteyn et al. 1987), and probably reflects the unusually wet summer of 1991. Although SWP and SWC of surface layers (< 0.3 m) were lower under large plants, there were no significant differences in pre-dawn XWP between small and large plants. This implies that there was no substantial difference in water availability between size classes during the summer growing season. If we reasonably assume similar leaf temperatures for both large and small plants, they did not differ in the use of water in response to drought. This response differs from that of some deep-rooted desert shrubs, where small individuals made less efficient use of water (Brown and Archer 1990; Donovan and Ehleringer 1992). However, small shrubs recovered photosynthetic rates faster than their larger counterparts, after the short drought periods that are characteristic of the summer in the Chihuahuan Desert. Post-drought values of P_{max} were similar to those obtained by Mooney et al. (1978) in the Sonoran Desert, but unstressed P_{max} was 15% higher for large shrubs, whereas maximum g_s was 38% higher.

Stomatal conductance was strongly related to VPD, as reported for other desert species such as honey mesquite (Nilsen et al. 1983). The construction of VPD response curves based on data from diurnal curves often

poses problems, because other variables such as temperature change concomitantly during a diurnal cycle. Mooney et al. (1978) reported that stomatal conductance of creosotebush was little affected by temperature within the range of temperature values we encountered on the diurnal cycles in this field study. It is therefore reasonable to conclude that stomatal conductance of creosotebush is affected by changes in leaf-to-air VPD. Changes in pre-dawn XWP were accompanied by changes in the slope of the VPD response curves and maximum values of g_s .

Although Meinzer et al. (1988) found no close relationship between maximum g_s and pre-dawn XWP in creosotebush, their values of pre-dawn XWP were low, ranging from -2.1 to -3.6 MPa. At this range of XWP, stomatal conductances were already low and the slope of the VPD response curve approached zero (Fig. 5). However, our results at higher XWP show, contrary to earlier suggestions (Odening et al. 1974) that creosotebush is apparently capable of effectively controlling water loss through stoma. The close relationship between g_s and CO_2 -exchange (Fig. 7), at PPFD values that are not limiting photosynthesis suggests that the observed decrease in photosynthetic rate during drought is affected by stomatal closure in response to water stress. Indeed C_i also decreased during the drought period. However, P_{max} remained fairly constant at pre-dawn XWP below -3 MPa, a result also reported for creosotebush in the Sonoran Desert (Odening et al. 1974), although they did not report g_s . At pre-dawn XWP of -4.5 MPa, a substantial P_{max} (about 20% of unstressed P_{max}) was maintained, whereas g_s was about 10% of unstressed values. A seasonal shift in temperature dependence of light saturated photosynthesis has also been reported to occur for creosotebush (Mooney et al. 1978).

There were large differences in the pattern of growth between small and large plants. The rate of stem length increase in large shrubs was similar to that reported for irrigated (25 mm month^{-1}) shrubs of similar size, at the same site (Fisher et al. 1988). Allocation to reproduction was a function of shrub size. Large creosotebush flowered and produced fruits during the summer, while flower and fruit production was not common for small plants. Reproduction may account for 50% or more of total aboveground production of creosotebush (Cunningham et al. 1979), and this may account for some of the difference in stem growth between large versus small plants. However, whether this difference between small and large plants is only a result of a shift in allocation pattern, or in resource limitation for the large plants, is unknown. Changes in allocation to roots might also influence reproductive effort. The decrease in growth observed during the months of September and October for both size classes was probably a result of the lower air temperatures and of decreased availability of soil water.

The results reported here suggest that creosotebush is capable of tight stomatal control in response to changes in environmental factors, allowing it to effec-

tively utilize the summer rains that are characteristic of the Chihuahuan Desert. Although creosotebush appears to be mainly responding to changes in water availability in the first 0.5 m of the soil profile, long-term survival may be more closely related to deep soil reserves. The control of stomatal opening in creosotebush appears to be a function of leaf-to-air VPD and plant internal water status, of which pre-dawn XWP is a good indicator. Small and large shrubs exhibited similar responses to environmental factors and the level of water stress in the dry spell was sufficient to markedly reduce CO_2 uptake perhaps through both stomatal (reduced C_i values) and non-stomatal mechanisms. Small shrubs were able to recover faster from short-term drought, an important response during the establishment phase. Models of productivity and physiological function for this species will have to take into consideration differences in growth between the establishing and established (mature) shrubs, which may be related to differences in allocation patterns.

Acknowledgements Phil Harrigan, Jacques Brisson, and Cathie Sandell provided invaluable field assistance. We are grateful to John Anderson for his logistical support. We thank W. H. Schlesinger and D. T. Kincaid for comments on early versions of this manuscript. David Tremmel provided assistance with the statistical analysis. This research was supported by National Science Foundation grant DEB 9006621 and it is a contribution to the National Science Foundation Jornada Long Term Ecological Research Program under Grant BSR 88-11160.

References

- Brown JR, Archer S (1990) Water relations of a perennial grass and seedling versus adult woody plants in a subtropical savanna, Texas, USA. *Oikos* 57:366-374
- Cannon WA (1911) The root habits of desert plants. Carnegie Institution of Washington 131:1-96
- Cui M, Smith WK (1991) Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. *Tree Physiol* 8:37-46
- Cunningham GL, Syvertsen JP, Reynolds JF, Willson JM (1979) Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cov. *Oecologia* 40:113-123
- Donovan LA, Ehleringer JR (1992) Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Functional Ecology* 6:482-488
- Fisher FM, Zak JC, Cunningham GL, Whitford WG (1988) Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *J Range Manage* 41:387-391
- Fonteyn PJ, Schlesinger WH, Marion GM (1987) Accuracy of soil thermocouple hygrometer measurements in desert ecosystems. *Ecology* 68:1121-1124
- Freckman DW, Virginia RA (1989) Plant-feeding nematodes in deep-rooting desert ecosystems. *Ecology* 70:1665-1678
- Kunkel KE, Malm NR, Earl RA (1990) Climate guide, Las Cruces 1851-1987. New Mexico State University Agricultural Experiment Station Research Report No.623
- Lajtha K, Whitford WG (1989) The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80:341-348

- Ludwig JA (1977) Distributional adaptations of root systems in desert environments. In: Marshall JK (ed) *The belowground ecosystem: A synthesis of plant-associated processes*. Range Sci. Ser. 26, Colorado State University, Fort Collins pp 85–91
- Meinzer FC, Rundel PW, Sharifi MR, Nilsen ET (1986) Turgor and osmotic relations of the desert shrub *Larrea tridentata*. *Plant Cell Environ* 9:467–475
- Meinzer FC, Sharifi MR, Nilsen ET, Rundel PW (1988) Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77:480–486
- Monson RK, Smith SD (1982) Seasonal water potential components of Sonoran Desert plants. *Ecology* 63:113–123
- Mooney HA, Björkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. *Plant Physiol* 61:406–410
- Nash MH, Daugherty LA (1990) Soil-landscape relationships in alluvium sediments in southern New Mexico. New Mexico State University Agricultural Experiment Station Bulletin No 746
- Nilsen ET, Sharifi MR, Rundel PW, Jarrell WM, Virginia RA (1983) Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran Desert of California. *Ecology* 64:1381–1393
- Nulsen RA, Bligh KJ, Baxter IN, Solin EJ, Imrie DH (1986) The fate of rainfall in a mallee and heath vegetated catchment in southern West Australia. *Aust J Ecol* 11:361–371
- Odening WR, Strain BR, Oechel WC (1974) The effect of decreasing water potential on net CO₂ exchange of intact desert shrubs. *Ecology* 55:1086–1095
- Oechel WC, Strain BR, Odening WR (1972a) Photosynthetic rates of a desert shrub, *Larrea divaricata* Cav., under field conditions. *Photosynthetica* 6:183–188
- Oechel WC, Strain BR, Odening WR (1972b) Tissue water potential, photosynthesis, ¹⁴C-labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. *Ecol Monogr* 42:127–141
- Pressland AJ (1976) Soil moisture redistribution as affected by throughfall and stem flow in an arid zone shrub community. *Aust J Bot* 24:641–649
- Reynolds JF (1986) Adaptive strategies of desert shrubs with special reference to the creosotebush. In: Whitford WG (ed) *Desert Ecology*. University of New Mexico Press, Albuquerque pp 19–49
- Schlesinger WH, Fonteyn PJ, Marion GM (1987) Soil moisture content and plant transpiration in the Chihuahuan Desert of New Mexico. *J Arid Environ* 12:119–126
- Sharifi MR, Meinzer FC, Nilsen ET, Rundel PW, Virginia RA, Jarrell WM, Herman DJ, Clark PC (1988) Effect of the manipulation of water and nitrogen supplies on the quantitative phenology of *Larrea tridentata* (creosotebush) in the Sonoran Desert of California. *Am J Bot* 75:1163–1174
- Sheps LO (1973) Survival of *Larrea tridentata* S&M seedlings in Death Valley National Monument, California. *Israel J Bot* 22:8–17
- Smith WK (1978) Temperature of desert plants: another perspective on the adaptability of leaf size. *Science* 201:614–618
- Shreve F (1942) The desert vegetation of North America. *Bot Rev* 8:195–246
- Strain BR (1969) Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. *Ecology* 50:511–513
- Strain BR (1970) Field measurements of tissue water potential and carbon dioxide exchange in the desert shrubs *Prosopis juliflora* and *Larrea divaricata*. *Photosynthetica* 4:118–122
- Syvrtsen JP, Cunningham GL, Feather TV (1975) Anomalous patterns of stem xylem water potentials in *Larrea tridentata*. *Ecology* 56:1423–142